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Perceptual Discrimination in Monkeys: Retroactive Visual Masking[1]

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ADKINS, J. W., L. G. FEHMI and D. B. LINDSLEY. *Perceptual discrimination in monkeys: retroactive visual masking.* PHYSIOL. BEHAV. 4(2) 255–259, 1969.—Five monkeys were trained to discriminate between a square and a triangle presented in a 5 msec tachistoscopic flash with 95–100 per cent accuracy. An essential feature of this trained performance was a programmed sequence of events in which the monkey learned to attend following self-triggering of the stimulus flash. When the monkeys had learned to make the perceptual discrimination with nearly 100 per cent accuracy, the test flash (T) presenting the patterns was followed by a nonpatterned blanking flash (B) at various interstimulus intervals (ISI). When the ISI was 40 msec or greater B had no effect on the perceptual discrimination of T and correct performance of the task remained at 95–100 per cent as in the case of T presented alone. At ISIs of 30–40 msec performance level decreased, suggesting partial masking of T by B; at ISIs of 15–25 msec performance in the visual discrimination task fell to a chance level indicating complete retroactive or backward masking of T by B. These results are in accord with human perceptual blanking or masking studies and have opened the way to investigation of the locus of visual masking by electrophysiological recording in the visual system of monkeys.

Temporal visual discrimination in monkeys Visual perception Perceptual masking

IT HAS long been known that the perception of a brief visual stimulus can be suppressed by the occurrence of a subsequent visual stimulus within a short critical interval [3, 9]. Such apparently retroactive perceptual interference has been extensively studied in human subjects; relevant literature has been reviewed by Alpern [2], Kietzman [14], and Raab [20], among others.

While many investigators of retroactive visual masking have attempted to relate their findings to known or hypothetical visual physiology, only recently have there been studies in which both psychophysical and electrophysiological measures were taken simultaneously. A recent series of studies [6, 7, 8] has investigated computer-averaged evoked potentials during perceptual interference in the visual system. Donchin and Lindsley [7] studied average evoked potentials recorded from the scalp over the visual association areas in human subjects during backward masking or, as it has been called, retroactive perceptual blanking. On the basis of their data they could only conclude, in the case of masking of perception of the first stimulus by the second where the evoked response to the first stimulus was displaced by the second, that the point of interference of the neural processes was at the visual cortex or at some more peripheral point in the visual pathways.

In order to investigate the locus of the interference, it obviously would be desirable to record evoked potentials from preceding stages of the visual system. If retroactive or backward masking could be demonstrated reliably in a laboratory animal, then chronically-implanted electrodes could be used to obtain such measures. Therefore, the present experiments were undertaken to develop and validate methods for training monkeys in a temporally-ordered visual discrimination task in which backward visual masking could be demonstrated and to record evoked potentials at various points along the visual pathways. This paper describes the training procedure and the behavioral results which show that backward visual masking comparable to that in man can be produced reliably in monkeys. The electrophysiological correlates of retroactive visual masking in monkeys are reported elsewhere [11, 18].

METHOD

Subjects

The subjects were five young monkeys, three male pigtailed macaques (*Macaca nemestrina*) and two stump-tailed macaques (*Macaca speciosa*), one male and one female.

Apparatus

The general layout of the apparatus is illustrated in Fig. 1. Shown on the right is the experimental chamber which contains the stimulus panels and the response manipulanda.

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The plastic chair in which the monkey lived was lifted from its rack and placed on the metal supports in the chamber. The wooden box to the left of the chamber contains the apparatus for projecting the stimuli upon the stimulus panels. The remainder of the equipment shown is for the programming, timing and monitoring of the sequence of stimuli and the recording of responses. At the far left is the EEG which, coupled with a tape recorder (not shown), was used for electrophysiological recording [11]. Figure 2 shows a close-up view of the stimulus panel and the behavior of a trained monkey in the experimental chamber.

General Procedures

At the beginning of the experiments, the monkeys were gradually adapted over a period of several weeks to living in restraining chairs. They remained in the chairs thereafter except for intermittent periods of a few days during which they were kept in individual cages.

Discrimination Training

The monkeys were trained to discriminate between tachistoscopically-presented black line-drawings of a square and an upright equilateral triangle. These two figures were projected simultaneously, each onto one of two translucent Lucite panels at eye level about 26 cm directly in front of the monkey, which was seated in a restraining chair inside a closed chamber (see Fig. 2). The stimulus panels, 4.5 cm wide by 7.5 cm high, were separated by a strip of plexiglass 1.3 cm wide. The dimensions of the patterns, which were projected onto the backs of the stimulus panels from 35 mm. slides, were 2.5 cm square for the square and 2.5 cm high and 2.5 cm wide, at the base, for the triangle. An exposure of the two stimulus figures will be called the "test flash" (T).

The projector was a Kodak Carousel (Model 550) which has a remote-controlled, rotating slide magazine. The projection lamp was replaced by a glow modulator tube (Sylvania R1131C). The light from the crater of the tube was projected onto a small mirror which re-directed the light upon the slide. Luminance of T was 15 mL.

The glow modulator tube was driven by a Tektronix 160A power supply and a specially constructed driver unit [4], triggered by a Tektronix 161 pulse generator. The exposure duration of T could be varied by adjusting the setting of the pulse generator. The duration and intensity of T were monitored by leading the output of a photocell, attached to the glow modulator tube, to a Tektronix Model 502 oscilloscope. In addition, the duration and amplitude of the triggering pulse from the pulse generator were monitored on the oscilloscope. The duration of this pulse also was measured on a Hewlett–Packard Model 522B electronic counter.

The stimulus panels served also as response manipulanda. When depressed, each closed a microswitch, completing a circuit which led to the subsequent events in the program. The square was always the correct stimulus and a press on the panel on which it appeared was rewarded on each trial by one 190 mg, banana-flavored food pellet (Ciba), delivered automatically to a tray at the right side of the stimulus panels. A press on the panel on which the triangle appeared was never rewarded. The position of the two figures was changed automatically from one panel to the other from trial to trial in a quasi-random sequence controlled by a program set on a stepping switch.

Since the animals were required to discriminate between briefly-exposed patterns, it was necessary to insure that their attention was directed toward the panels at the moment when T appeared. To accomplish this, the animals were trained to trigger T themselves, by pressing and releasing a lever at the right side of the stimulus panels. T was triggered automatically 300 msec following the release of this lever. Immediately following either a correct or an incorrect panel press, a dim overhead light was turned on automatically and signalled the beginning of a fifteen sec inter-trial interval, during which both the lever and the stimulus panels were inactivated. At the end of this inter-trial delay, the offset of the overhead light indicated that a press and release of the lever now would cause T to appear.

During initial training on the discrimination problem, T, once triggered, was flashed repetitively at a duration and frequency well above the values which yielded flicker fusion for humans and remained on until the monkey had pressed one of the panels. When an animal had learned the discrimination to a criterion of 90 per cent correct responses, T was changed to a single flash, whose duration was reduced day by day from an initial value of one sec. Training was continued until the animal consistently made 90–100 per cent correct responses at a T duration of 5 msec.

At this time, repeated measurement of T duration thresholds were carried out by gradually reducing T duration within daily training sessions. The T durations at which accuracy consistently fell below 90 per cent were shorter than 0.5 msec. for all the animals. Thus, the five-msec T duration used during most of the subsequent testing was well above the duration threshold. The thresholds were of the same order of magnitude as human thresholds obtained in the same apparatus. Further details of the training procedure have been described elsewhere [1].

Tests for Backward Masking

Following about one week of overtraining on the 5 msec T, a "blanking flash" (B) was introduced. B consisted of a bright, unpatterned illumination of the panels for about 20 μsec by a flash from a Grass PS–2 photostimulator set at Intensity 16 (peak luminance 10^5 mL). During most of the testing, B occurred following T on approximately half of the trials in a session. Trials on which T was succeeded by B will be called TB trials. The remaining trials, on which T was presented alone, served as control trials and will be called T trials. The occurrence of B was determined by a stepping-switch program designed to eliminate any contingency between reward and irrelevant events in the testing sequence. The test for backward masking was a comparison of correct responses when T occurred alone and when it was followed, at various intervals, by B. Testing was carried out in daily sessions of 99–198 trials, varying from animal to animal and with amount of training, but was held constant for each animal within a given test series. A noncorrection training procedure was used. The monkeys were given their food ration shortly after the daily testing and were fed at no other time.

During the initial tests for backward masking, the occurrence of B had little effect on the number of correct responses at IFIs greater than about 50 msec. Therefore, most of the subsequent testing was done with B following T at intervals ranging from 5 msec (B onset simultaneous with T offset) to 50 msec. The IFI was constant within a daily testing session but was reduced in steps from session to session. This descending series was repeated several times for each animal and discrimination performance was recorded on T alone trials and TB trials during each session. Right, left, and

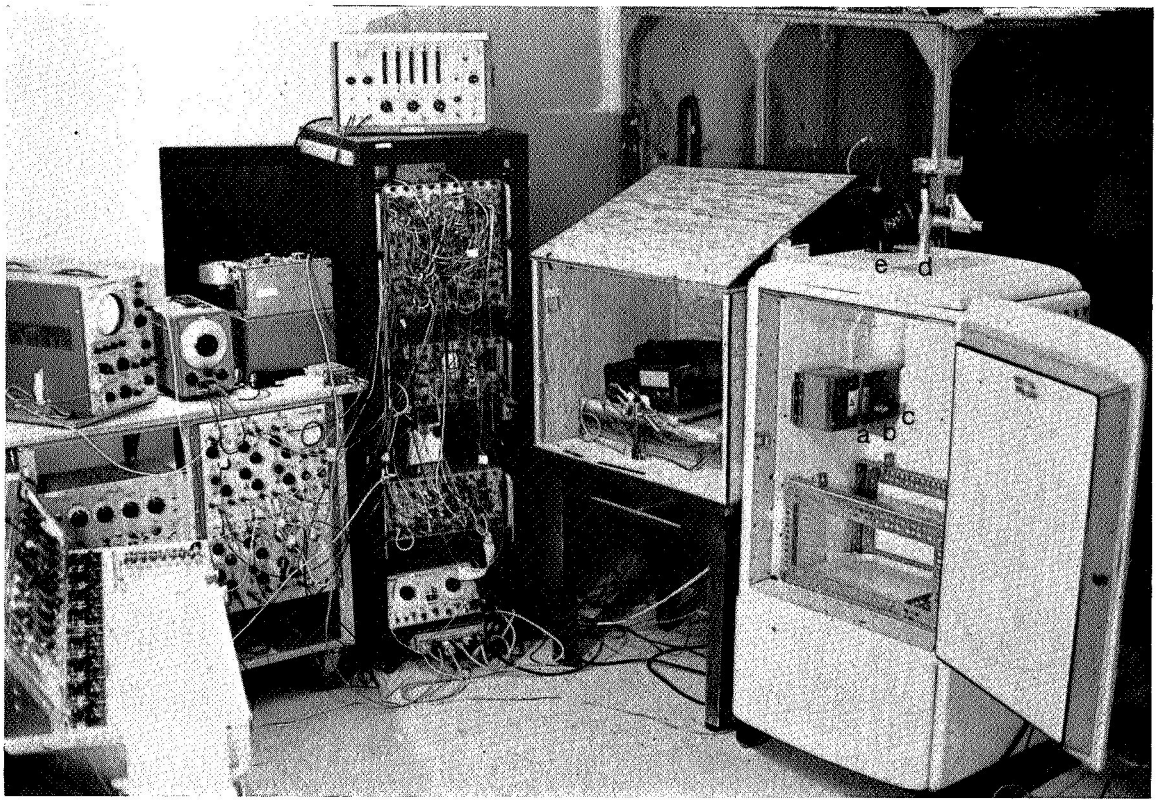

FIG. 1. General experimental arrangement. Right to left: Experimental chamber, a—stimulus and response panels, b—reward pellet cup, c—set-up lever to trigger stimuli, d—automatic pellet dispenser, e—ventilator fan; stimulus projection box; equipment rack for controlling, monitoring, and recording programmed stimulus-response events; oscilloscope, oscillator, camera and pulsing and timing devices; EEG.

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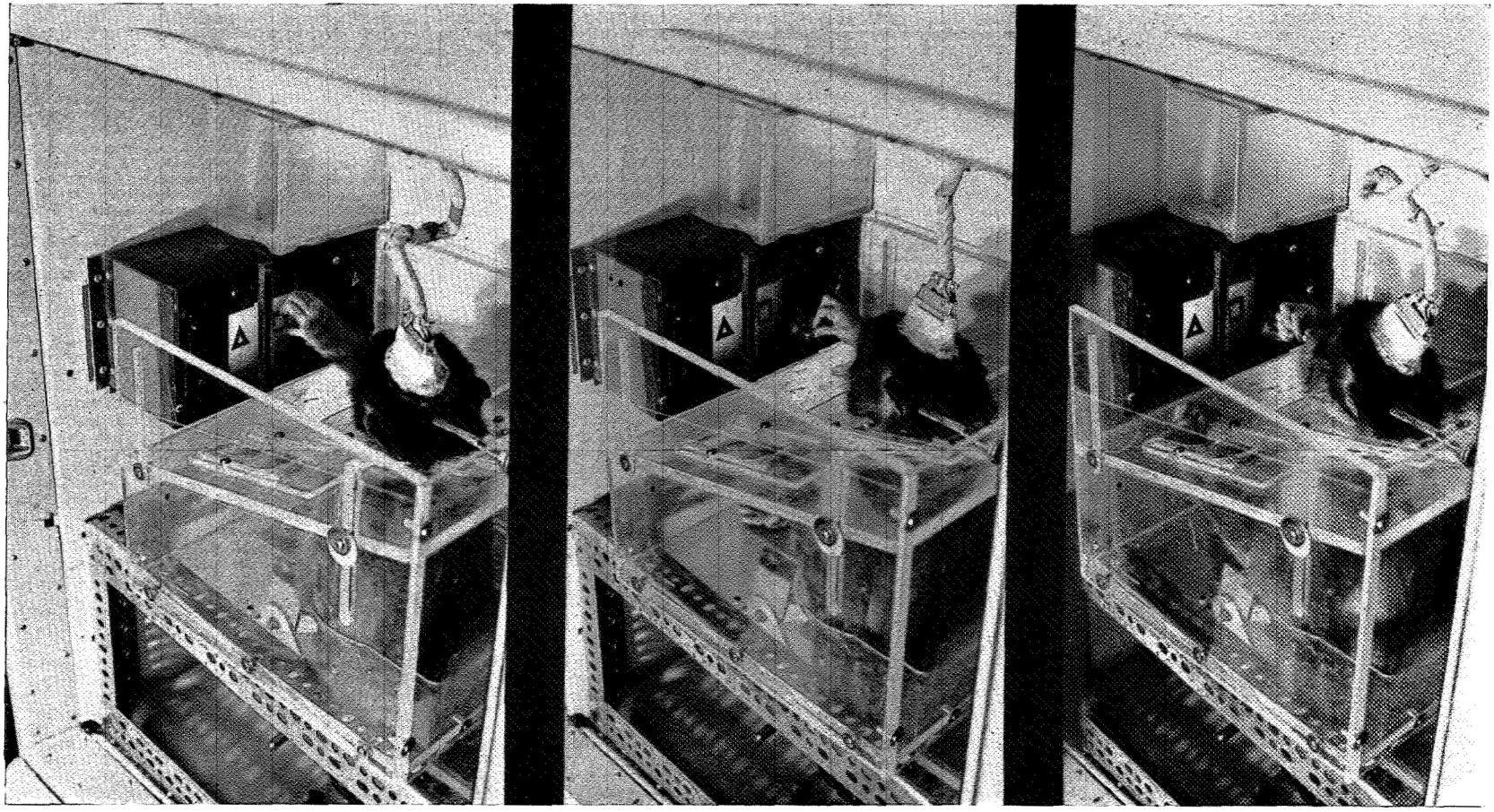

FIG. 2. Close-up of monkey in experimental chamber, pressing correct stimulus panel, retrieving banana pellet reward and eating it. Normally patterns on stimulus panels are present for only 5 msec and have disappeared before animal presses the panel. Dim overhead light comes on for 15 sec following either correct or incorrect press; when light goes out monkey must press and release the set-up lever at right of reward cup to receive another stimulus presentation.

correct responses were registered separately for T and TB trials on electromechanical counters and on an event recorder.

The IFI was controlled by a Tektronix pulse generator and could be varied by adjusting the delay setting. The length of the interval was monitored on the electronic counter by measuring the delay between the pulse which triggered T and that which triggered B and was adjusted to the chosen value before each session. In addition, the same photocell which was used to monitor T also responded to B and the IFI thus could be measured on the oscilloscope as well.

The programming equipment used to control the automated sequence of events in the testing program was a series of relays, pulse formers, stepping switches, and timers manufactured by the Davis Scientific Instrument Co., plus the Tektronix waveform and pulse generators. Further description of the apparatus is given by Adkins [1] and Fehmi [10].

RESULTS

Since each animal served as his own control, the results are presented separately. In Figs. 3 and 4, the percentage of correct responses on masking (TB) trials is plotted against the delay between the two flashes (IFI). Percentages for control, T-alone, trials (stars), intermixed with TB trials at each ISI, are also shown in Fig. 3. The graphs represent test series carried out following several weeks of training in the backward masking situation. In earlier test series, accuracy had improved considerably with practice. The data shown here are typical of the stabilized performance of highly-trained animals.

Figure 3A shows the average performance of Smoothie, a male *Macaca nemestrina*, on five test series at a T duration of 5 msec. Each plotted point represents about 150 trials for the TB data and about 350 trials for the T data. At IFIs of 40 or 50 msec, performance on TB trials was at control levels, that is, the same as for T alone trials. Previous tests had shown that there was no decrease in accuracy at IFIs of 75, 100, 125, 150, 200, or 300 msec. As the IFI was reduced below 40 msec, however, there was a marked decline in accuracy on TB trials and performance fell to chance levels at IFIs below about 20 msec. Performance on control trials (T alone) remained at close to 100 per cent accuracy throughout the series. Thus there is clear evidence of backward masking of T by B, the interference increasing as the IFI was reduced.

Figure 3B shows a similar average curve for Nasty, another male *Macaca nemestrina*, also tested at a T duration of 5 msec. In this case, discrimination performance was little affected by the occurrence of B on TB trials at IFIs above 30 msec. As the interval was reduced, there again was a decrease in accuracy on TB trials and the IFI at which chance performance was reached was similar to that found for the previous monkey (below 20 msec). Figure 3B also indicates the variability of performance for Nasty over four test series. The vertical lines represent one standard deviation above and below the mean. Variability measures are not shown for the T trials since performance was invariably at or above 95 per cent. While the variability shown in Fig. 3B is typical of performance over many repeated series, it should also be noted that inter-series variance decreased with practice. Therefore, the plotted standard deviations overestimate the final, stable variance.

Figure 3C and D represent the performances, respectively, of Raunchy, a male, and Prissy, a female, *Macaca speciosa*. Each curve represents a single descending test series with 99 trials a day—51 T and 48 TB trials. There appears to be no striking difference between the performance of these two stump-tailed macaques and that of the pig-tailed macaques shown in Fig. 3A and B. All the curves are similar, both in

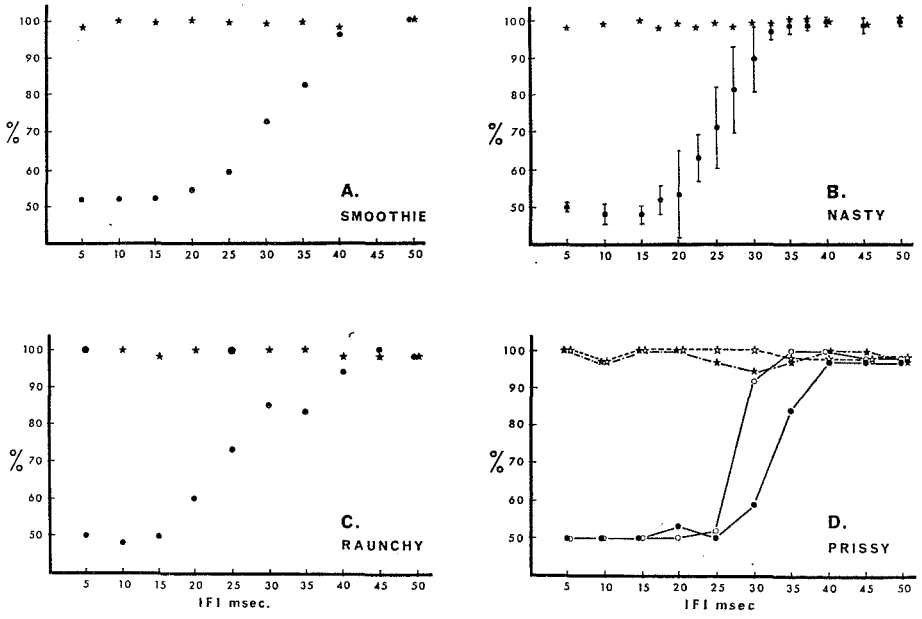

FIG. 3. Performance graphs for four monkeys showing per cent correct responses for TB trials (dots) where test flash (T) is followed by blanking flash (B) at interflash interval (IFI) shown on abscissa, and for T alone trials (stars). In B bars show typical variability (± 1 SD). In D solid and open symbols are for series of trials run more than two weeks apart. (See text for further explanation)

their general form and in the range of IFIs over which masking occurred.

In Fig. 3D, curves for two descending series for Prissy are plotted separately to illustrate further the variability in performance from one series to another. For all the animals, performance at a given IFI varied somewhat from series to series but the general form of the curve remained the same. Complete series, when repeated, were always at least two weeks apart and in some cases were separated by several weeks.

With respect to the data presented in Fig. 3, it may be said for all four animals that performance in discriminating the square from the triangle ranged from 95–100 per cent correct during T-alone trials. On TB trials in which the blanking flash followed the test flash at IFIs of 40 msec or greater, performance remained at the same high level and did not differ significantly from T-alone trials. However, as the IFI on TB trials decreased from 40 msec there was in each case a progressive decrease in the correctness of performance on the visual discrimination task until the animal's performance was at a chance level (50 per cent). Decrement in performance for each animal began at IFIs of 30–35 msec and reached chance level at IFIs of 15–25 msec.

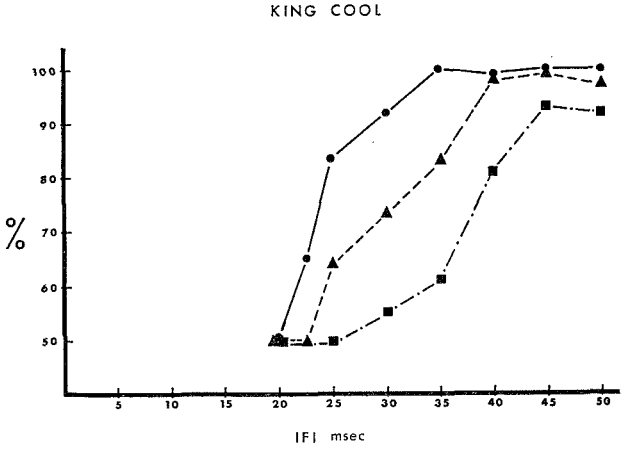

FIG. 4. Performance graph for monkey King Cool on TB trials where T duration was varied on successive days: dots—5 msec, triangles—2.5 msec, squares—1 msec. Ordinate: per cent correct discriminations; abscissa: interflash interval (IFI). (See text for explanation)

Figure 4 shows the effect on backward masking of reducing T duration. These data were obtained from King Cool, a third male *Macaca nemestrina*. Starting at an IFI of 50 msec, the animal was tested at each IFI at T durations of 5.0, then 2.5, and then 1.0 msec on successive days. Tests were carried out in daily sessions of 198 trials and each plotted point represents 96 TB trials. The remaining 102 T trials have been omitted to simplify the graph: accuracy on these control trials never fell below 97 per cent in any session at any of the three T durations. On the TB trials, at IFIs within the range where partial masking occurred, accuracy was poorer the shorter the T duration. Reducing T duration thus increased the backward interference produced by B.

DISCUSSION

Backward Masking. The results of these backward masking experiments with monkeys are quite consistent with earlier studies of human subjects, for example, by Lindsley and Emmons [16, 17]; Lindsley [15]; Kietzman [14]; Donchin [6]; and also Raab [20]. Accuracy on the discrimination problem decreased when the exposure of the patterns was followed within a critical interval by a brief, unpatterned illumination of the stimulus panels. As in human studies, the amount of interference within this interval was a monotonic function of the temporal separation of T and B, accuracy decreasing as the inter-stimulus interval was shortened.

Our data from monkeys agree closely with human results reported by Lindsley [15] in a study which, like the present one, used a flash from a Grass photostimulator (intensity setting 16) for B and a black-on-white pattern for T. He found the IFI above which masking no longer occurred to be about 40 msec and the IFI below which accuracy was at chance levels to be 20–30 msec (depending upon intensity of B), values very close to those found in the present study, using roughly comparable intensity values for T and B. Kietzman [14], Boyle [4], and Donchin [6] have reported generally similar results. It should be noted that the range of IFIs over which T is masked depends on several variables, including the relative intensities and durations of the test and masking stimuli, as well as on the task required of the subject [cf. 14, 20]. Therefore, little general significance can be attached to the absolute values of the critical interval for masking.

The backward masking curves for the monkeys also are quite like those found for a human subject in the same apparatus. For the human, at a T duration of 5 msec, there was some interference at IFIs of about 30–32 msec. At IFIs below about 23–25 msec, T was not identified more frequently than expected by chance. The range of IFIs over which accuracy fell from 100 to 50 per cent was typically only about 7 or 9 msec for the human while, as can be seen in Figs. 3 and 4, it usually was somewhat greater for the monkeys.

Test-flash duration thresholds. The exposure durations of the simultaneously presented patterns at which highly accurate discrimination performance was obtained are considerably shorter than those which have been reported in previous studies of tachistoscopic discrimination in monkeys. However, a recent study by Pribram *et al.* [19] has indicated that differential discrimination of successively presented patterns can be made when each pattern is presented for durations as short as 0.01 msec. As was mentioned earlier, the durations in the present study at which accuracy fell below 90 per cent were shorter than one-half msec. On the other hand, Chow and Orbach [5] found that performance on a tachistoscopically-presented color discrimination was between 70 and 80 per cent correct at exposures of 10–20 msec and was less than 90 per cent correct at an exposure of 40 msec. They also trained their animals on a pattern discrimination but accuracy as a function of T duration was not reported. Fuster and Uyeda [13], using as stimuli solid objects briefly illuminated by a flash from a glow modulator tube, reported that the average performance of their monkeys was only slightly above chance at a 10 msec exposure and was less than 75 per cent correct at 40 msec. Fuster [12] previously had reported near-chance performance at 10 msec, about 70 per cent accuracy at 20 msec, and about 85 per cent correct at durations as long as 40 msec.

While any of a number of variables might be expected to affect tachistoscopic discrimination performance, it seems

likely that the accuracy attained by our monkeys was largely a consequence of the self-programming procedure which allowed the monkeys themselves to trigger T. In fact, observation of trained monkeys at work in this situation showed that they focus their attention upon the stimulus area when they press and release the lever. In the studies mentioned above, on the other hand, T was presented automatically following a warning signal. Two of our monkeys also were originally trained with the stimuli presented at a fixed interval following a warning signal (the offset of an overhead light). Their accuracy remained at only 75–80 per cent at T durations as long as 75–100 msec, even after about four weeks of training in which they received several thousand trials. The procedure was then changed to permit self-programming and accuracy was greater than 95 per cent at a T duration of only 5 msec within a week after the animals had learned to use the set-up lever. Thus, it appears that tachistoscopic performance is greatly facilitated by allowing the animals themselves to trigger the stimuli, which it is believed enables them to learn to establish and maintain an appropriate attentional set.

In summary, these experiments establish, first, that monkeys can be trained to discriminate reliably between patterns presented for durations so short as to approach the threshold range for humans. Second, backward visual masking is readily demonstrable in monkeys and appears similar to the perceptual interference found in human subjects under comparable conditions.

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